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Observations on Abnormal Shoot Growth in Betula pendula Roth.

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Summary

Observations on a form of abnormal shoot growth are reported and compared with normal shoot growth in *Betula pendula*. The abnormality appears as a portion of shoot with enhanced multiplication and compaction of stem units. The abnormalities, termed HAM shoots, are closely linked to the production of male catkins and it is postulated that they represent a malfunction of a gene reaction system incorporating both vegetative and reproductive characteristics. The observations are presented with a view to increase the limited knowledge concerning the genetic control of plant growth and development.

Key words: *Betula pendula*, shoot growth, floral development, genetic control of growth.

Zusammenfassung

Es wird über Beobachtungen über anomales Sproßwachstum im Vergleich mit normalem Sproßwachstum bei *Betula pendula* berichtet. Die Anomalie tritt als Sproßteil mit mehr und kompakteren Zweig-Einheiten auf. Die Anomalien, sogenannte HAM-Sprosse, sind mit der Produktion männlicher Kätzchen eng verbunden; es wird postuliert, daß sie eine Funktionsstörung eines Gen-Reaktionssystems mit sowohl vegetativen wie auch reproduktiven Merkmalen darstellen. Die Beobachtungen werden in der Absicht vorgelegt, die begrenzten Kenntnisse der genetischen Kontrolle von pflanzlichem Wachstum und pflanzlicher Entwicklung zu erweitern.

Introduction

Betula pendula Roth. together with other species of arborescent birch shows clearly defined shoot forms which fall into four categories:

1. Proleptic long shoots formed by predetermined growth only, that is from the expansion of bud contents laid down during the previous season. In the reproductive areas of mature trees such shoots produce the terminal male catkins.

2. Proleptic long shoots formed initially from predetermined growth, but further extension growth occurs due to indeterminate growth. This latter growth is derived from a currently active terminal meristem where leaves and internodes are initiated and expand without pause.

3. Sylleptic long shoots which emerge on the indeterminate shoot portions of vigorous, low order type two shoots. These shoots are produced by the outgrowth of newly laid down axillary meristems and in very infrequent cases, sylleptic shoots may also bear further sylleptic shoots.

4. Short shoots formed by the predetermined production of 2—5 compacted internodes on lateral axes of long shoots. These 'dwarf' shoots are the site of female catkin production in mature trees.

The general morphology of these shoots types in shown in *Figure 1*.

In all tree species shoot formation is regular and predictable and in consequence tree crowns are highly organis-

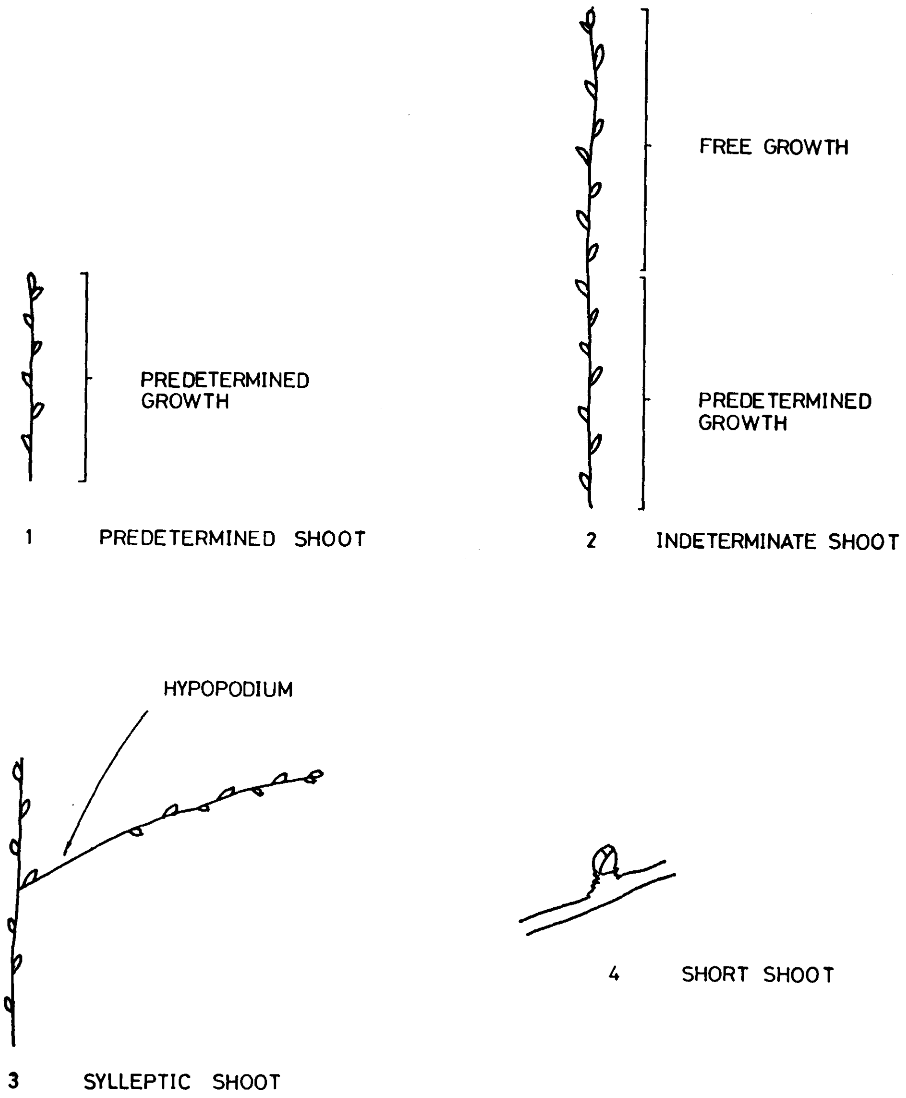

Figure 1. — General morphology of birch shoots.

ed structures with only subtle differences between species. However in a great many broadleaved species very rare individuals are found that have major changes in crown form. Common examples are fastigiate or weeping cultivars prized and clonally propagated by horticulturalists.

A review of the literature has shown that instances of modification of the above four shoot forms within birch crowns in particular and tree crowns in general has either not been observed or has attracted little critical attention. The single exception in birch is the frequently observed shoot proliferation known as 'witches broom' brought about by a localized infection of the fungus *Taphrina turgida* SADEB. (PEARCE, 1962).

MASTERS (1968) and WORSDELL (1916) described in great detail the morphology of numerous teratological plant structures and in some cases interpreted these in terms of atavism. HALL (1984) instances three descriptions of atavistic structures:

1. a 'tendency to reproduce the ancestral type';
2. a 'reversion to a previous evolutionary state'; and
3. a 'throwback'.

All three phrases in HALL's interpretation embodied the essential features of the atavistic character and, although his study was concerned with a wide range of animal species, his definitions are also applicable to plants.

One of the best known studies on plant teratology was that of HESLOP-HARRISON (1952) who concluded that major abnormalities of plant growth may shed light on the origin of normal growth and that for example, failure of hormonal systems could result in the development of structures that were intermediate between leaves and floral parts. MEYER (1966) in an extensive review of floral abnormalities referred to the fact that, after 1900, reports on this subject are few yet these structures are potentially valuable in the study of organ differentiation.

WARDLAW (1957) suggested that developmental genes were activated only when the physiological situation was suitable for their activity and that the plant meristem acted as a reaction system involving the sequential switching on and off of a series of genes. In his conclusions Wardlaw considered that the study of the morphological implications of the system presented problems in that little was known about the possibility of its experimental modification.

An understanding of the processes involved in the development and differentiation of both vegetative and reproductive structures is essential to tree breeders and those physiologists who are concerned with the control of flowering in tree species. The observations below on abnormal shoot structures that appear to represent a transition between vegetative and reproductive growth are presented in the hope that they offer an insight into the study of phase change in trees.

Materials and Methods

The shoot growth abnormalities reported here were observed and recorded in a progeny test of *B. pendula* over a three year period. The test seedlots were raised in 1978 and consisted of 1,730 trees from the open pollinated progeny of 100 selected mother trees located mainly in north-east Scotland, but additional seedlots were obtained from Scandinavia, western Europe and England. The test site lies seven kilometres west of Aberdeen on a fertile, clear-felled area at an altitude of about 150 metres. Establishment of the large, polythene tunnel grown seedlings in terms of survival was very high, 97% at four years of age and height increment although variable was frequently between 70 and 100 centimetres during the first season.

The first female flowers appeared during the year of planting (1979) and by the late summer of that year male catkins were produced on a small number of trees. In order to restrict the study to typical *B. pendula*, those identified as natural hybrids (Brown, Kennedy and Williams, 1982) and two precocious families were excluded from the results presented here, leaving a population of 1,622 trees. The period of study between 1979 and 1981 covered the transition during which the population was leaving the juvenile vegetative phase and entering a more mature and

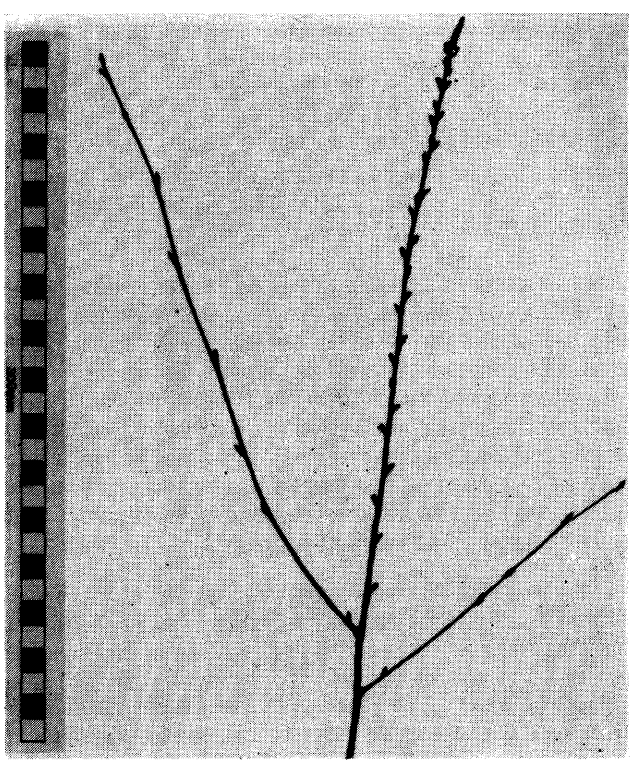

Figure 2. — A dormant HAM shoot.

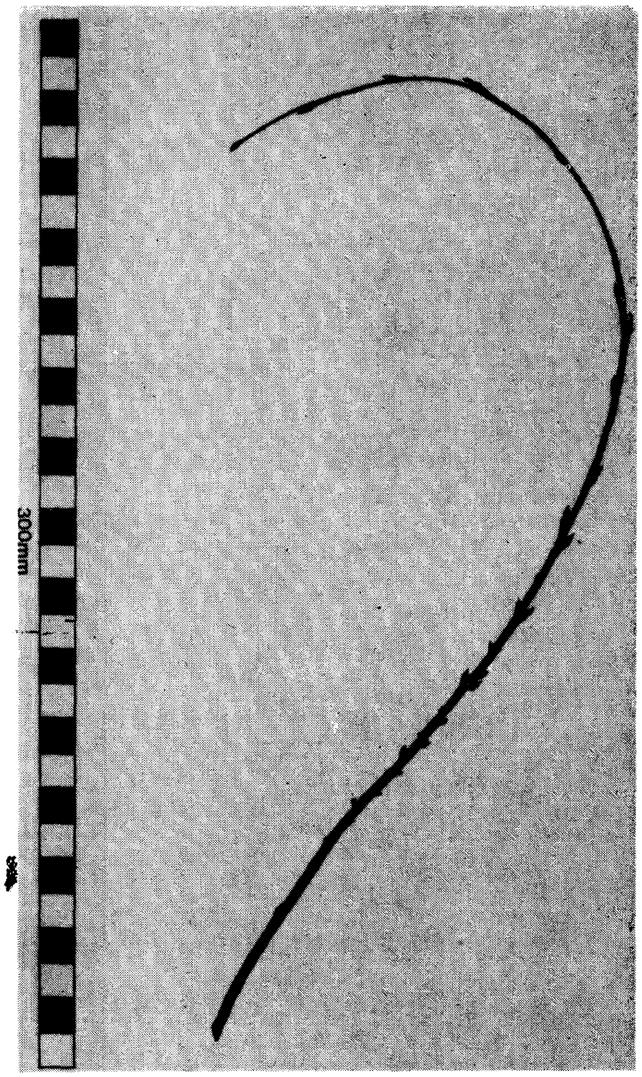

Figure 3. — A type 2 long shoot with a central HAM section.

reproductive stage of development. As part of routine observations the incidence of flowering was recorded annually and during these inspections shoot abnormalities were also noted. The reproductive status of the population increased dramatically between 1981 and 1984 but precise records were not kept during this period. However, observations were continued on the incidence of abnormal shoot development and a collection of herbarium specimens made.

Observations and Discussion

The abnormalities under consideration here have been termed by the author as HAM shoots due to the fact that their immediate cause appears to be the activity of a hyper-active meristem. A typical abnormal shoot is presented in *Figure 2* which shows the compacted nature of the terminal stem units of which there are in excess of 30.

At the distal end of the shoot, axillary buds are replaced by male catkins and a male catkin terminates the shoot. The unifying feature of all the structures reported here is the enhanced multiplication of stem units. The degree and duration of multiplication is variable and as is shown in *Figure 3* may occupy only a portion of the entire shoot.

Up to the end of 1981, 32 trees (2%) in the progeny test were found to have one or more HAM structures and 21 trees (1.3%) were recorded as having produced male catkins, thus at this stage of the progeny test both characters were infrequent. Cross referencing records for individual trees showed that 12 of the trees with HAM shoots also had produced male catkins. The probability of a single tree having a HAM shoot is $p = 0.02$ and that for a male catkin is 0.013, however, the probability of a single tree having both a HAM shoot and a male catkin is the product of the above, ie. $p = 0.00026$ which is a statistically very low chance of this event occurring. As indicated above a number of trees (12) were found on which both male catkins and HAM shoots were present. The probability of these 12 events occurring in the defined population is $p = 4.34^{-14}$ and this level is so low that it would appear that the two phenomena are very closely linked.

Due to the infrequent and almost unpredictable incidence of HAM shoots little is known about their ontogeny except that which may be inferred from the collected specimens. *Table 1* presents information on the basic morphological characteristics of 30 specimes of HAM shoots. From these results it can be seen that HAM structures are borne on indeterminate shoots (categories two and three), and a high proportion of these produced female flowers within the compacted area. Lateral buds within the HAM section of the shoot almost invariably produce short shoots although, if the distal buds are vegatative, these normally elongate to continue the main axis. In consequence, HAM structures do not terminate the growth of a shoot but in subsequent years the apex continues to elongate and the HAM region produces normal radial growth. In those HAM structures of more than two years of age the only visible sign of the abnormality is a series of swellings signifying the positions of dead short shoots.

The extent of the affected area varies considerably within the range of 43—310 mm and this is reflected in the

Table 1. — Morphology of 30 preserved 'HAM' specimens.

1. Growth characteristics of bearing shoot	
Indeterminate	24
Determinate	0
Unknown	6
2. Association with reproductive structures	
Male catkins on HAM	2
Female catkins on HAM	7
Structure too young or no association	21
3. Growth arising from lateral buds along HAM axis	
Long shoot growth	0
Short shoot growth	19
Combination of above	3
Not determined	8

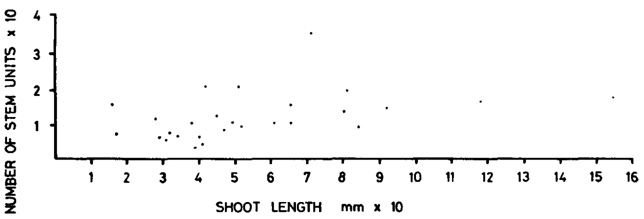

Figure 4. — The relationship between HAM length and number of compacted stem units.

range of multiplication, from 8—71 units. *Figure 4* shows the relationship between HAM structure length and the number of compacted stem units. The correlation at $r = 0.45$ is significant at $p = 0.01$ but as shown by the scatter diagram this relationship is affected by several outliers.

From *Table 1* it can be seen that HAM structures are initiated on long shoots (ie. category two shoots) following the period of predetermined growth and so would be undergoing multiplication at a time when male catkins are also developing in similar terminal positions on predetermined long shoots, (category one shoots). This observation suggests that the union between the normal long shoot and HAM structure is comparable to that of the union between the predetermined long shoot and male catkin. Abbe (1983) undertook a comprehensive study of the range of variation in floral and inflorescence morphology in the *Betulaceae* and commented, 'In the following pages reference is made to the transition region from twig to ament. In some genera this region, which is immediately below the ament proper, often exhibits interesting and significant deviations from the morphological conditions in the ament. It is the region in which the internodes are progressively shorter, the leaves smaller, and the buds sometimes replaced by floral structures'. The range of floral variation Abbe reported was extensive but he found no comparable structures to those reported above. The observations discussed here also indicate the significance of what Abbe termed the transition region.

As early as 1790 Goethe postulated that all the appendices of leafy shoots which encompass leaves, bracts, sepals, petals, stamens and pistils are homologeous. This theory, together with that of Wardlaw (1957) suggests that the HAM structure, closely linked to the production of male catkins in trees at the transition from juvenility to maturity are in fact unsuccessful attempts to produce male catkins. Dormant male catkins consist of a compacted pedicel bearing waxy protective bracts and bracteoles subtending groups of anthers (Abbe, 1974). In its dormant form the male catkin is between five and 20 mm in length and comprised of between 50 and 150 laternal units and so in morphological terms there is a degree of similarity between HAM structures and male catkins.

The association between reproductive structures and HAM shoots is evident from *Figures 1* and *5* where both lateral female and lateral male catkins are present. Normally the siting of the different sexes within the shoot system is very regular, but Tolstopyachenko (1974) considered that the sex determination of individual flowers in birch was unstable and this conclusion was also indicated by Abbe (1938).

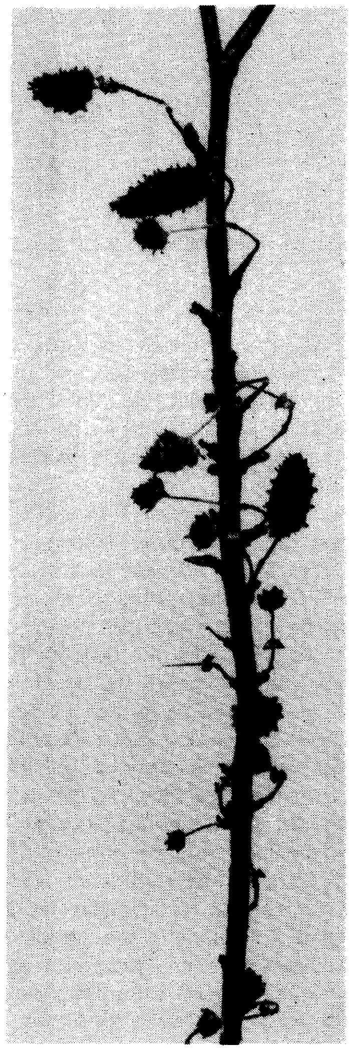

Figure 5. — Two year old HAM shoot bearing numerous female catkins.

The foregoing discussion relates only to an association between HAM shoots and male catkins, but in one instance the shoot shown in *Figure 6* was produced from an over-wintering lateral bud. The lower part of the shoot expanded and produced a large number of vestigial leaves, the lower ones with axillary buds and the upper ones with miniture but complete axillary female catkins. A normal sized female catkin terminated the shoot which had developed in a compacted form inside an exillary bud. This single structure indicates a similar, but much rarer, apparent instability in the development of female catkins.

The causal agents which trigger the production of these shoots abnomalities is unknown, however Bloch (1953) presented six possible agents which caused growth abnormalities and of these three, namely injury, growth substance treatment and irradiation do not appear plausible in the present cases. The fourth agent, that of parasitic infection has already been discussed and such shoot proliferation, known as 'witches broom', is clearly distinct from the HAM shoots. A recent comprehensive volume (Phillips and Burdekin, 1982) covering both living and non-living agents causing tree disorders, describes 'witches broom' in birch, but structures similar to those reported here were not observed (Burdekin, pers. comm.). The final two causal agents reported by Bloch encompass a wide but poorly defined range of influences namely general nutritional and physiological disturbances, and hereditary constitution. From the growth of the progeny test trees there has been no suggestion of nutritional stress and within any tree the occurrence of HAM structures are isolated and infrequent events even when male catkin production was prolific. This localized occurrence does not preclude a genetic component to their initiation but supports the theory that HAM structures are the expression of a combination of reproductive and vegetative growth characteristics.

Conclusions

The instances of abnormal growth reported here form a coherent group marked by the anomolous production of compacted stem units with reduced or irregular leaves. The HAM structures are both morphologically and statistically closely linked to the production of male catkins and appear to be composed of both reproductive and vegetative components. It has not been possible to identify the stimulus that triggers this form of shoot growth but it appears to involve the localized activation of a reaction system as postulated by Wardlaw (1957). The value of structural abnormalities to the study of developmental plant anatomy was emphasised by Heslop-Harrison (1952) and Meyer (1966) and the observations reported here, although not fully

Figure 6. — A birch shoot terminated by a normal male catkin, but also bearing the abnormal contents of a dormant lateral bud.

conclusive, support this principle but, based on the definitions of Hall (1984) the HAM shoots do not represent an ativistic development.

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Inheritance of Allozymes in a Black Spruce Diallel Cross

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Summary

Methods developed in our laboratory for extracting and characterizing electrophoretic variants of enzymes from needle tissues were used in this study for the analysis of the genetic control of allozyme variants of a 7 × 7 black spruce diallel cross. From this controlled mating scheme 1,066 progeny were analyzed. Of the 16 enzymes tested, seven (AAT, ACO, GDH, LAP, MDH, PGM, and SDH) produced phenotypes that were variable and had banding patterns that possessed good activity and high resolution. For one of these enzymes (AAT), two variable loci were present.

Key words: allozymes, inheritance, *Picea mariana*, pedigree certification, electrophoresis, somatotyping.

Zusammenfassung

In dieser Studie wurden in unserem Labor entwickelte Methoden zur Gewinnung und Charakterisierung elektrophoretischer Enzymvarianten aus Nadelgeweben zur Analyse der genetischen Kontrolle von Allozymvarianten eines 7 × 7 Kreuzungs-Diallels mit *Picea mariana* angewandt. Aus diesem kontrollierten Kreuzungsschema wurden 1066 Nachkommen analysiert. Von den 16 getesteten Systemen produzierten 7 (AAT, ACO, GDH, LAP, MDH, PGM und SDH) Phänotypen, die variabel waren und Bandmuster hatten, die eine gute Aktivität und eine hohe Festigkeit besaßen. Für eines dieser Enzymsysteme (AAT) waren 2 variable Loci vorhanden.

Introduction

Black spruce (*Picea mariana* [Mill.] B.S.P.) grows in all 10 provinces and two territories of Canada. It is a commercially important species, as the long fibres make this tree highly desirable to the pulpwood industry. A specific mating design, the diallel cross, was initiated by Morgenstern (1974) at the Petawawa National Forestry Institute for the purpose of evaluating variance components such as those due to selfing, maternal, and reciprocal effects. In this report we examine the isozyme composition of progeny from a 7 × 7 black spruce diallel cross that was established at Petawawa in 1973. We used techniques that were developed in our laboratory for the extraction of enzymes from vegetative tissues of conifers (Pitel and Cheliak, 1984; Cheliak and Pitel, 1984a). The purpose of the study was to demonstrate the genetic control of allozyme polymorphisms at seven loci of black spruce. In addition, we describe other enzyme systems of black spruce that either lacked variation or whose starch gel phenotypes were difficult to interpret. Isozyme analysis also indicated that some progeny of a cross did not have the expected genotype compositions, suggesting contamination. The use of isozymes as simple ge-

FEMALE PARENT

MALE PARENT	29	52	59	60	62	63	65
29	M	14	M	16	17	18	19
52	M	21	22	23	24	25	26
59	27	28	29	30	31	32	33
60	34	35	36	37	38	39	40
62	41	42	43	44	45	46	47
63	48	49	50	51	52	53	54
65	55	56	57	58	59	M	61

Figure 1. — Design of the controlled mating scheme used for seven black spruce trees and the cross numbers allocated to each cross. "M" indicates that the cross was missing.

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